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SHORTER ARTICLES AND DISCUSSION

ON THE RESULTS OF INBREEDING A MENDELIAN POPULATION: A CORRECTION AND EXTENSION OF PREVIOUS CONCLUSIONS¹

IN a recent paper by the present writer on inbreeding,² the conclusion was reached (*loc. cit.*, p. 608)

that no increase in the proportion of homozygotes in the population follows inbreeding save under one or the other of two special conditions, viz.:

(a) Continued self-fertilization.

(b) Some form of gametic assortative mating which increases the natural probability of like gametes uniting to form zygotes.

This conclusion is entirely correct as it stands, but also barren, for it overlooks the very essential fact that any sort of inbreeding involves in greater or less degree "gametic assortative mating." The mathematical demonstration on page 608 of the paper referred to is also entirely correct so far as it goes, but it stops too soon. Up to the third generation of brother $\times$ sister mating starting from a population of complete heterozygotes there is no increase in the proportion of homozygotes beyond that prevailing in a general Mendelian population. In the fourth and later generations there is, however. The blunder, kindly pointed out to me by Professor E. M. East, which in retrospect seems altogether too stupid even to be possible, was in the failure to recognize that after the second generation the constitution of the *family* would no longer be the same as that of the population. This is the point which makes illegitimate the extension by induction of the results up to the third generation to the generations beyond.

The general conclusion of the former paper quoted above, should then be as follows: An increase in the proportion of homozygotes in the population will follow inbreeding of any sort, though at different rates for different types of inbreeding, *because any inbreeding involves homogamy (or assortative mating) in some degree.*

Having made clear the location and nature of the error I desire now to show in some detail exactly what results follow from con-

¹ Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 54.

² "A Contribution Towards an Analysis of the Problem of Inbreeding," AMERICAN NATURALIST, Vol. XLVII, pp. 577-614, 1913.

tinued brother $\times$ sister mating in a Mendelian population. To this we may now proceed.

THE DISTRIBUTION OF A MENDELIAN POPULATION IN SUCCESSIVE
GENERATIONS WITH CONTINUED BROTHER $\times$ SISTER
MATING

Let us start with a population composed entirely of complete heterozygotes. We shall consider a single character pair, A denoting the dominant character, and a the recessive. The complete heterozygote individual will then be Aa , and will produce in equal numbers A and a gametes.

In making an analysis of the effect of inbreeding on the population it will be necessary to deal not merely with the distribution of individuals in each generation, but also with the distribution of families of the several types. Each mating will produce an array of families, as well as an array of individuals. The standard family throughout this discussion is taken as including 32 individuals, of which 16 are males and 16 females. It is further assumed that there is no sex-linkage of characters, and that in any family there will be an equal number of brothers and sisters of each zygotic constitution represented. One family of 16 pairs of brothers and sisters will make 16 matings and produce 16 families of 32 individuals each. This constant rate of fertility is assumed throughout the discussion.

Every mating made is of a brother with his sister.

With so much by way of preliminary definition of the limitations of this investigation, let us proceed to the actual analysis.

First Generation

Constitution of the Population.—By hypothesis all individuals are Aa .

Proportion of Homozygotes in this Generation.—0 per cent. of the whole population.

Matings to Produce the Second Generation.—Start with one brother $\times$ sister pair of individuals from this population. The mating will be $Aa \times Aa$. This will produce *one family*, $8AA + 8Aa + 8aA + 8aa$.

Second Generation

Constitution of the Population.— $8AA + 8Aa + 8aA + 8aa$.

Proportion of Homozygotes in this Generation.—50 per cent. of the whole population.

Matings to Produce the Third Generation.—The matings of the one family of this generation will be as follows:

$\sigma^1 \sigma^1$	$\varphi \varphi$	$\sigma^3 \sigma^3$	$\varphi \varphi$
(1) AA	(1) AA	(9) aA	(3) aA
(2) AA	(5) AA	(10) aA	(7) aA
(3) AA	(9) AA	(11) aA	(11) aA
(4) AA	(13) AA	(12) aA	(15) aA
(5) Aa	(2) Aa	(13) aa	(4) aa
(6) Aa	(6) Aa	(14) aa	(8) aa
(7) Aa	(10) Aa	(15) aa	(12) aa
(8) Aa	(14) Aa	(16) aa	(16) aa

Third Generation Families Produced.—(Note: the numbers in parenthesis are to identify matings and their consequent families.)

	AA	Aa	aA	aa
(1)	32			
(2)	16	16		
(3)	16	16		
(4)		32		
(5)	16		16	
(6)	8	8	8	8
(7)	8	8	8	8
(8)		16		16
(9)	16		16	
(10)	8	8	8	8
(11)	8	8	8	8
(12)		16		16
(13)			32	
(14)			16	16
(15)			16	16
(16)				32

Third Generation

Constitution of the Population.—

$$128AA + 128Aa + 128aA + 128aa.$$

Proportion of Homozygotes in this Generation.—50 per cent. of the whole population.

Fourth Generation Families Produced.—The third generation families, when mated, will produce families as follows:

Summarized this gives the following fourth generation *families* produced:

- (1)₄ 36 families like (1)₃
 (2)₄ 24 families like (2)₃

- (3)₄ 4 families like (4)₃
 (4)₄ 24 families like (5)₃
 (5)₄ 80 families like (6)₃
 (6)₄ 24 families like (8)₃
 (7)₄ 4 families like (13)₃
 (8)₄ 24 families like (14)₃
 (9)₄ 36 families like (16)₃

	AA	Aa	Aa	aa
Family (1) ₃ will produce . . 16 families of constitution	32			
Families (2) ₃ will produce 4 families of constitution	32			
(3) ₃ , (5) ₃ will produce . . . +4 families of constitution	16	16		
and (9) ₃ will produce . . . +4 families of constitution	16		16	
each will produce +4 families of constitution	8	8	8	8
Families (4) ₃ will produce 16 families of constitution	8	8	8	8
and (13) ₃				
each				
Families (6) ₃ will produce. 1 family of constitution	32			
(7) ₃ , (10) ₃ will produce . . +2 families of constitution	16	16		
and (11) ₃ will produce . . +1 family of constitution		32		
+2 families of constitution	16		16	
+4 families of constitution	8	8	8	8
+2 families of constitution		16		16
+1 family of constitution			32	
+2 families of constitution			16	16
+1 family of constitution				32
Families (8) ₃ will produce 4 families of constitution	8	8	8	8
(12) ₃ , (14) ₃ will produce . . +4 families of constitution		16		16
and (15) ₃ will produce . . +4 families of constitution			16	16
each will produce +4 families of constitution				32
Family (16) ₃ will produce 16 families of constitution				32

Fourth Generation

Constitution of the Population.—

$$2560AA + 1536Aa + 1536aA + 2560aa.$$

Proportion of Homozygotes in this Generation.—62.5 per cent. of the whole population.

Fifth Generation Families Produced.—The third generation families, when mated, will produce families as follows:

- (1)₄ will produce $36 \times 16 = 576$ families like (1)₃
 (2)₄ will produce $24 \times 4 = 96$ families like (1)₃
 + 96 families like (2)₃
 + 96 families like (5)₃
 + 96 families like (6)₃
 (3)₄ will produce $4 \times 16 = 64$ families like (6)₃
 (4)₄ will produce $24 \times 4 = 96$ families like (1)₃
 + 96 families like (2)₃
 + 96 families like (5)₃
 + 96 families like (6)₃

(5) ₄ will produce	80	families like (1) ₃
	+ 80 × 2 = 160	families like (2) ₃
	+ 80	families like (4) ₃
	+ 160	families like (5) ₃
	+ 80 × 4 = 320	families like (6) ₃
	+ 160	families like (8) ₃
	+ 80	families like (13) ₃
	+ 160	families like (14) ₃
	+ 80	families like (16) ₃
(6) ₄ will produce	24 × 4 = 96	families like (6) ₃
	+ 96	families like (8) ₃
	+ 96	families like (14) ₃
	+ 96	families like (16) ₃
(7) ₄ will produce	4 × 16 = 64	families like (6) ₃
(8) ₄ will produce	24 × 4 = 96	families like (6) ₃
	+ 96	families like (8) ₃
	+ 96	families like (14) ₃
	+ 96	families like (16) ₃
(9) ₄ will produce	36 × 16 = 576	families like (16) ₃

Summarized this gives the following fifth generation families produced:

(1) ₅	848 families like (1) ₃
(2) ₅	352 families like (2) ₃
(3) ₅	80 families like (4) ₃
(4) ₅	352 families like (5) ₃
(5) ₅	832 families like (6) ₃
(6) ₅	352 families like (8) ₃
(7) ₅	80 families like (13) ₃
(8) ₅	352 families like (14) ₃
(9) ₅	848 families like (16) ₃

$$4096 (= 16 \times 256).$$

Fifth Generation

Constitution of the Population.—

$$44,736AA + 20,480Aa + 20,480aA + 44,736aa.$$

Proportion of Homozygotes in This Generation.—68.75 per cent. of the whole population.

Sixth generation families produced:

17,216	families like (1) ₃
4,480	families like (2) ₃
832	families like (4) ₃
4,480	families like (5) ₃
11,520	families like (6) ₃
4,480	families like (8) ₃
832	families like (13) ₃
4,480	families like (14) ₃

17,216 families like (16)₃

65,536 ($= 16 \times 4,096$).

Sixth Generation

Constitution of the Population.—

786,432AA + 262,144Aa + 262,144aA + 786,432aa.

Proportion of Homozygotes in This Generation.—75 per cent. of the whole population.

From this point on it will not be necessary to carry out the work in detail. The final results are given in Table I for four more generations.

TABLE I

SHOWING THE CONSTITUTION OF THE POPULATION AFTER 7 TO 10
GENERATIONS OF BROTHER $\times$ SISTER MATING

Gener- ation	AA	Aa	aA	aa	Percentage of Homozy- gotes in Whole Pop- ulation
7	13,369,344	3,407,872	3,407,872	13,369,344	79.69
8	224,395,264	44,040,192	44,040,192	224,395,264	83.59
9	3,724,541,952	570,425,344	570,425,344	3,724,541,952	86.72
10	61,337,501,696	7,381,975,040	7,381,975,040	61,337,501,696	89.26

It is evident that the proportion of homozygotes is approaching 100 per cent. in the same manner as in the case of self-fertilization, worked out by East, Jennings and others, but at a slower rate.

In a later paper I hope to take up the problem of the general formulæ for finding the constitution of a Mendelian population after n generations of inbreeding of the different types, and at the same time discuss the relation of these results to the coefficients of inbreeding described in my former paper. It should be specifically mentioned that, in the light of the data here set forth, those criticisms of the conclusions of East and Hayes made in my former paper³ which were based on the erroneous assumption of a fundamental difference between self-fertilization and all other forms of inbreeding in respect to homozygosis, have no validity whatever. It scarcely needs to be said that the blunder on the theoretical side here corrected in no wise affects the usefulness of inbreeding coefficients.

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³ Cf. Pearl, *loc. cit.*, p. 606, 609 and 610.